Biotypic Variation Among North American Russian Wheat Aphid (Homoptera: Aphididae) Populations

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ABSTRACT The Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), has been a major economic pest of small grains in the western United States since its introduction in 1986. Recently, a new Russian wheat aphid biotype was discovered in southeastern Colorado that damaged previously resistant wheat, *Triticum aestivum* L. Biotype development jeopardizes the durability of plant resistance, which has been a cornerstone for Russian wheat aphid management. Our objective was to assess the relative amount of biotypic diversity among Russian wheat aphid populations collected from cultivated wheat and barley, *Hordeum vulgare* L. We conducted field surveys from May through June 2002 and August 2003 from seven counties within Texas, Kansas, Nebraska, and Wyoming. Based upon a foliar chlorosis damage rating, three new Russian wheat aphid biotypes were identified, one of which was virulent to all characterized sources of Russian wheat aphid resistance. The future success of Russian wheat aphid resistance breeding programs will depend upon the continual monitoring of extant biotypic diversity and determination of the ecological and genetic factors underlying the development of Russian wheat aphid biotypes.

KEY WORDS biotype, plant resistance, *Diuraphis noxia*, *Triticum aestivum*

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), is one of the more economically important and widely distributed pests of wheat, *Triticum aestivum* L., and barley, *Hordeum vulgare* L. (Stoetzel 1987). A native of central Asia (Durr 1983), it now occurs, except for Australia, throughout the major small grain production areas of the world. It is believed to have reached the United States in 1986 from the northward movement of populations originating near El Batan, Mexico (Gilchrist et al. 1983).

In the United States, economic infestations occur annually, and where resistant varieties are not available, are primarily controlled by insecticides. Reliance on chemicals to control Russian wheat aphid has been mitigated by the development and deployment of resistant cultivars, particularly in wheat production areas prone to Russian wheat aphid infestations (Berzonsky et al. 2002). However, the recent discovery of a new Russian wheat aphid biotype in Colorado that is virulent to all currently deployed Russian wheat aphid-resistant cultivars has raised major concerns regarding durability of future Russian wheat aphid resistance sources (Haley et al. 2004). Of particular concern was the finding that the newly discovered Russian wheat aphid biotype was virulent to eight of the nine known Russian wheat aphid resistance gene sources.

Biotypic variation has been known to occur among Russian wheat aphid populations for some time. Based on differential responses of a limited number of plant resistance sources, Puterka et al. (1992) found eight Russian wheat aphid isolates from a worldwide collection to be biotypically unique. Since then, Russian wheat aphid biotypic variation has been recognized among populations in Hungary (Basky 2003) and Chile (Smith et al. 2004). However, biotypic variation had not been detected from surveys conducted in the United States until March 2003 when Russian wheat aphid-resistant winter wheat grown in southeastern Colorado was severely damaged (Shufran et al. 1997, Haley et al. 2004). The discovery of this new biotype jeopardizes wheat production in areas where resistant cultivars have served as the cornerstone for Russian wheat aphid management. The objective of this study was to assess the relative amount of biotypic diversity among Russian wheat aphid populations collected from cultivated wheat and barley throughout the United States Great Plains.

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Table 1. Collection sites, hosts, sampling date, and no. of samples of Russian wheat aphids used to assess biotypic variation

State	County	Location[a]	Host	Sample date	No. aphid samples
Kansas	Marshall	Marysville	Wheat	June 2002	10
Nebraska	Gage	Beatrice	Wheat	June 2002	10
	Lincoln	North Platte	Wheat	June 2002	4
Texas	Floyd	Floydada	Wheat	May 2002	10
	Lubbock	Idalou	Wheat	May 2002	10
Wyoming	Big Horn	Emblem	Barley	Aug. 2003	5
		Lovell	Barley	Aug. 2003	5
		Worland	Barley	Aug. 2003	10
	Park	Powell	Barley	Aug. 2003	10

[a] Location given is the nearest town or city.

Materials and Methods

Collections in the Field. Russian wheat aphids were collected during May through June 2002 and August 2003 from seven counties within Texas, Kansas, Nebraska, and Wyoming (Table 1). A minimum of 10 fields, separated by a minimum distance of 3.2 km, in each county were sampled using a Stihl model 85 leaf blower-vacuum (Stihl Incorporated, Virginia Beach, VA) customized to function as a D-vac system by modifying the vacuum tube (10 cm in diameter) to accept a fine mesh collection bag. This system made it possible to precisely sample specific locations on the plants and facilitated the sampling of a large number of plants in a short period. Samples were collected from cultivated wheat and barley displaying Russian wheat aphid damage symptoms. All plants sampled were in the heading stage of development (GS 10–11, Feekes scale; Large 1954), and the aphids were exposed and easily collected from the spikes. Collected Russian wheat aphids were transferred from the collection bag to 'Schuyler' barley seedlings that were then enclosed within ventilated, clear plastic cylinder cages to prevent sample contamination. Subsequent clonal test colonies for biotypic evaluation were established by selecting a single, apterous Russian wheat aphid from each sample. Test colonies were reared on Schuyler barley grown in caged pots and maintained in environmental chambers with a photoperiod of 16:8 (L:D) h at 20 and 18°C, respectively.

Determination of Biotype. The biotypic status of each test colony was determined using nine previously established plant resistant sources containing designated resistance genes *Dn1* through *Dn9* (Table 2) and three susceptible wheat cultivars, 'Custer', 'TAM 105', and 'Yuma'. In addition to the test colonies, a founder colony, which was established in 1987 from Russian wheat aphids collected from Bailey County, TX (Webster and Starks 1987), and considered to be the original north American Russian wheat aphid biotype (Russian wheat aphid-1), was evaluated to provide a basis for identifying biotypic variants. Five seeds of each plant entry were planted in separate 15-cm rows in a fritted clay medium in greenhouse flats in a randomized complete block design with five replications for each biotype evaluation. Plant entries were randomly assigned to rows and were separated by intervening border rows planted with Russian wheat aphid-susceptible TAM 105. Before testing, each Russian wheat aphid test colony was increased to ensure an adequate aphid population for testing. Immediately after planting, the flats containing the test plants were caged to ensure that secondary aphids would not contaminate the plants. The caged plants were infested as soon as they emerged, ≈1 wk after planting, by cutting heavily infested leaves from colonized plants and placing them next to each row of test plants. The tests were conducted in a greenhouse, using supplemental artificial light with a photoperiod of 16:8 (L:D) h, at 22 ± 5°C. Approximately 18–21 d after infestation, plant damage was qualitatively evaluated by rating the relative amount of foliar chlorosis and leaf rolling. Chlorosis was measured using a 1–9 rating scale (Burd et al. 1993), with 1, healthy looking plant; 2, isolated chlorotic spots; 3, chlorosis ≥5% but <20%; 4, chlorosis ≥20% but <35%; 5, ≥35% but <50%; 6, ≥50% but <65%; 7, ≥65% but <80%; 8, ≥80%; and 9, plant death. Based on this scale, we arbitrarily ascribed a damage score of 1 to indicate high resistance (HR); scores of 2 through 4 to indicate resistance (R); a score of 5 to indicate intermediate resistance (IR); scores of 6 through 8 to indicate susceptibility (S); and a score of 9 to indicate high susceptibility (HS). Leaf rolling was rated as either flat (F) or rolled (R), where the later refers specifically to convolutely rolled leaves that form the characteristic Russian wheat aphid induced leaf gall. This leaf gall results from the prevention of newly formed leaves from unfolding (Burd et al. 1998). After each test, insect vouchers were collected and deposited at the Cereal Insect Genetic Resource Library, USDA–ARS, Plant Science Research Laboratory, Stillwater, OK.

Table 2. Russian wheat aphid gene symbols and resistance sources used for biotype determination

Resistance designation	Source	Reference
Dn1	PI 137739	Du Toit (1987)
Dn2	PI 262660	Du Toit, (1987)
dn3	CO 03810	Nkongolo et al. (1989)
Dn4	Yumar	Quick et al. (1991)
Dn5	CO 950043	Du Toit, (1988)
Dn6	CI 6501	Harvey and Martin (1990)
Dn7	94M370	Marais et al., (1998)
Dn8	Karee-*Dn8*	Liu et al. (2001)
Dn9	Betta-*Dn9*	Liu et al. (2001)

Table 3. Damage ratings of Russian wheat aphid resistant sources infested with the Texas-1, Texas-2, Wyoming-1, and RWA-1 biotypes

Resistance source	Damage score			
	Texas-1	Texas-2	Wyoming-1	RWA-1
Dn1	7.2bA	6.3bA	6.6bA	6.3bA
Dn2	8.0aA	7.3aAB	6.4bB	3.8cdC
dn3	6.6bcA	7.1abA	7.3bA	3.2dB
Dn4	6.2cA	4.7cB	3.8cBC	3.0dC
Dn5	8.1aA	7.2aA	4.7cB	4.9cB
Dn6	8.1aA	4.3cB	4.6cB	4.3cdB
Dn7	6.9bA	6.5bA	3.8cB	4.8cB
Dn8	8.7aA	8.4aA	8.9aA	6.9abB
Dn9	8.4aA	8.1aAB	8.1abAB	7.1aB
Yuma	7.6abA	7.6aA	3.9cB	7.7aA
Custer	8.4aA	7.6aAB	8.4aA	7.2abB
TAM 105	8.1aA	7.7aA	8.5aA	7.6aA

Means within columns followed by the same lowercase letter and within rows followed by the same uppercase letter no not differ at the 0.05 level of probability (Fisher protected LSD).

Table 4. Summary of plant reactions to Russian wheat aphid biotypes

Resistance source	Resistant–susceptible reaction				
	Texas-1	Texas-2	Wyoming-1	RWA-1	RWA-2[a]
Dn1	S	S	S	S	S
Dn2	S	S	S	R	S
dn3	S	S	S	R	M[b]
Dn4	S	R	R	R	S
Dn5	S	S	R	R	S
Dn6	S	R	R	R	S
Dn7	S	S	R	R	R
Dn8	S	S	S	S	M[b]
Dn9	S	S	S	S	S
Yuma	S	S	R	S	S
Custer	S	S	S	S	S
TAM 105	S	S	S	S	S[c]

[a] From Haley et al. (2004).
[b] Moderately resistant.
[c] TAM 107 was used as a susceptible control.

Data analysis and computations were done with SAS (SAS Institute 1999) by using the analysis of variance procedure, and when appropriate, means were separated by Fisher protected least significant difference (LSD) test ($P \leq 0.05$).

Results and Discussion

From May through June 2002 and August 2003, Russian wheat aphids were collected from 74 wheat and barley fields from seven counties within four states to assess their biotypic diversity (Table 1). The sample locations were selected to encompass the peripheral margins of the primary latitudinal range of the Russian wheat aphid in the United States (Elliott et al. 1998). In 2002, Russian wheat aphid densities were extremely high in Floyd and Lubbock counties, TX, particularly in wheat planted in the water-stressed corners of fields using center-pivot irrigation. In contrast, Russian wheat aphid densities were very low in Lincoln County, NE, and were found in only four of the 10 sampled wheat fields. Population densities varied at the other sample locations, however, Russian wheat aphids were not difficult to locate and were present in all fields sampled. It should be noted that the collection of Russian wheat aphid from Gage County, NE, constituted a new county record.

Based on mean chlorosis damage-rating scores for all nine resistance sources, three new biotypes, which differed significantly from the scores for the original Russian wheat aphid biotype (Russian wheat aphid-1), were clearly evident among the Russian wheat aphid populations tested (Table 3). The new biotypes were Texas-1, collected from wheat in Floyd County, TX; Texas-2, collected from wheat in Lubbock County, TX; and Wyoming-1, collected from barley in Park County, WY. Moreover, damage ratings for the three new biotypes differ from those reported for the recently described Russian wheat aphid biotype 2 (Table 4), which was virulent or intermediately virulent to the same resistance sources except for *Dn7* (Haley et al. 2004).

The Texas-1 isolate was virulent to all Russian wheat aphid-resistant sources (Table 3). The wheat entries containing the *Dn1*, *dn3*, *Dn4*, and *Dn7* resistance genes scored significantly lower ratings than those for the susceptible controls; nonetheless, they exhibited foliar chlorosis on at least 50–65% of their total leaf areas. The Texas-2 isolate was virulent to all but the *Dn4* and *Dn6* entries, and although *Dn1* and *Dn7* were rated susceptible, their damage scores were significantly lower than those for the other susceptible-scored entries. The Wyoming-1 isolate was the least virulent of the new biotypes, having chlorosis scores ≥5.0 only on the *Dn1*-, *Dn2*-, *dn3*-, *Dn8*-, and *Dn9*-resistant entries. Chlorosis scores for the *Dn8* and *Dn9* resistance sources were similar to those for the susceptible entries Custer and TAM 105. Surprisingly, the Wyoming-1 isolate was avirulent to the susceptible control plant Yuma. The original Russian wheat aphid biotype (Russian wheat aphid-1) was only virulent on *Dn1*-, *Dn8*-, and *Dn9*-resistant sources and the susceptible entries, and although the *Dn1*-resistant source rated susceptible, its rating was significantly lower than those of the susceptible control plants.

Biotypic relationships for the Russian wheat aphid isolates, including Russian wheat aphid biotype 2, based upon resistant or susceptible designations assigned to the chlorosis damage scores for all characterized plant resistant sources are shown in Table 4. Overall, none of the resistant or susceptible plant sources rated HR (damage score 1) or HS (damage score 9). The mean chlorosis ratings ranged from 3.0 to 8.9; however, none of the mean damage ratings observed were within the range for IR (damage score 5.0–5.9). Thus, all ratings were designated either R or S.

Leaf rolling ratings for Texas-1, TX-2, WY-1, and Russian wheat aphid-1 are shown in Table 5. Leaf rolling is an important damage criterion because the resulting pseudogall is linked to the biological fitness of the Russian wheat aphid (Burd et al. 1993), and because the rolled leaf traps the subsequent emerging leaf, thereby arresting further plant development

Table 5. Leaf rolling rating for Russian wheat aphid biotypes

Resistance source	Leaf rolling rating			
	Texas-1	Texas-2	Wyoming-1	RWA-1
Dn1	R	F	F	F
Dn2	R	R	R	R
dn3	R	R	R	R
Dn4	R	R	R	F
Dn5	R	R	R	R
Dn6	R	F	F	F
Dn7	F	F	F	F
Dn8	R	R	R	R
Dn9	R	R	R	R
Yuma	R	R	R	R
Custer	R	R	R	R
TAM 105	R	R	R	R

(Burd et al. 1998). In the current study, we considered leaf rolling to have occurred if any of the plants of a tested cultivar were convolutedly rolled. The *Dn7*-resistant source was the only entry that did not exhibit leaf rolling, and the Texas-1 isolate was the only biotype to induce leaf rolling on the *Dn1*- and *Dn6*-resistant sources. There was little or no correspondence between chlorosis damage ratings and leaf rolling. Overall, five susceptible reactions had flat leaves, and seven resistant chlorosis reactions had rolled leaves (Tables 3 and 5). These results are consistent with previous studies where no significant correlations between chlorosis and leaf rolling were observed (Burd et al. 1993, Smith et al. 2004).

Although leaf rolling is an important damage criterion, it was not used for biotype determination because infested wheat seedlings often succumb before the initiation of new leaves, which are a requisite for convolutedly rolled leaves. Nonetheless, this does not diminish the importance of leaf rolling as a primary selection criterion for plant resistance breeding.

Because the new Russian wheat aphid isolates have unique virulence profiles when tested on *Dn*-designated plant resistant sources, we propose that the Texas-1 isolate to be designated Russian wheat aphid biotype 3 (Russian wheat aphid-3), TX-2 to be designated Russian wheat aphid biotype 4 (Russian wheat aphid-4), and Wyoming-1 to be designated Russian wheat aphid biotype 5 (Russian wheat aphid-5). Moreover, we propose that the Russian wheat aphid founder colony collected from Bailey County, TX, in 1987, and maintained at the USDA–ARS, Plant Science Research Laboratory in Stillwater, be designated Russian wheat aphid biotype 1 (Russian wheat aphid-1), and the *Dn-4*-virulent Russian wheat aphid biotype reported by Haley et al. (2004) be designated Russian wheat aphid biotype 2 (Russian wheat aphid-2).

In conclusion, it is generally agreed that an aphid biotype is an infraspecific population, independent of geographic distribution, that is able to injure a plant containing specific resistant gene(s) that are resistant to other infraspecific populations. Moreover, there is no presumption of the genetic basis within the aphid for the ability to cause injury, nor is any evolutionary or taxonomic status implied. Clearly, there are genetic differences among aphid biotypes, which affect feeding behavior and the phenotypic response of the plant. However, the term biotype does not describe those differences nor does it require knowledge of the biotype-specific traits that induce the damage symptoms. Consequently, the designation of Russian wheat aphid biotypes is based solely on the phenotypic response (i.e., foliar chlorosis) of the plant as a direct result of aphid feeding.

We have designated three new Russian wheat aphid biotypes that were collected from cultivated wheat or barley throughout the United States Great Plains. The new biotypes were differentiated using damage ratings based on Russian wheat aphid-caused foliar chlorosis on all characterized resistant gene sources and were designated Russian wheat aphid-3, Russian wheat aphid-4, and Russian wheat aphid-5. Russian wheat aphid-1 is the original biotype that has been maintained as a founder colony at the USDA–ARS, Stillwater, since 1987, and Russian wheat aphid-2 was recently documented in Colorado where it was found damaging *Dn4*-resistant wheat (Haley et al. 2004).

The biotypic status of all five of these Russian wheat aphid isolates can be resolved by comparing chlorosis ratings on three of the resistant sources, *Dn3, Dn4,* and *Dn7*. Overall, the *Dn4*-, *Dn6*-, and *Dn7*-resistant sources provided the widest range of resistance to the new biotypes; however, none of the resistant sources tested conferred a high level of resistance to Russian wheat aphid-3. Moreover, use of the current germplasm line containing the *Dn7* gene, which is the only documented resistance to Russian wheat aphid-2, may be restricted because of grain quality problems associated with 1BL.1RS wheat-rye translocation carrying the *Dn7* resistance gene (Haley et al. 2004). New sources of resistance to Russian wheat aphid-2 have recently been identified (Collins et al. 2005; Porter et al. 2005), and the search for additional sources of resistance to the newly identified Russian wheat aphid biotypes continues.

The low cost of host plant resistance to insects, both to the environment and to the grower, combined with the ease of putting it into production, make it an ideal method to manage Russian wheat aphids. However, pivotal to the future success of Russian wheat aphid resistance is the need to assess the amount of Russian wheat aphid genetic diversity for virulence and to understand the ecological and genetic bases of biotypic variation and its relationship to Russian wheat aphid fitness.

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